# THE EFFECT OF THE REMOVAL OF MICROTUS PENNSYLVANICUS ON AN OLD FIELD PLANT COMMUNITY

Thesis for the Degree of M. S.

MICHIGAN STATE UNIVERSITY

NORMAN GEOFFREY WEILERT

1972

# THE EFFECT OF THE REMOVAL OF *MICROTUS PENNSYLVANICUS* ON AN OLD FIELD PLANT COMMUNITY

by

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology

1972

## ACKNOWLEDGMENTS

The author wishes to express his most sincere appreciation to Dr. Rollin H. Baker, Michigan State University, for his advice and constructive criticism during this study and manuscript preparation. A debt of gratitude is also due to Drs. Peter Murphy and William Cooper and graduate students Peter Dalby, Jerry Hall, and Gary Dawson for their help in manuscript preparation. I offer thanks to Dr. John A. King for allowing me to use the six-year experimental plots and to Dr. Walter Connely for his aid in the statistical analysis of data. I am indebted to numerous people in the Botany Department for their help in identifying plant species.

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# ABSTRACT

In order to determine the influence of *Microtus pennsylvanicus* upon an old field community, vegetation samples were collected at three week intervals during the summer of 1971 from a plot from which *Microtus* had been excluded for six years and from a newly constructed plot. Control plots, to which *Microtus* had free access, were compared to each of the exclosure plots. Ten samples were collected from each area for every sampling period, and the values recorded include: the number of plant species, percentage of the total biomass of *Bromus inermis*, weights of *Bromus* and *Poa* spp., total biomass, height of each *Bromus* individual, and weight of litter. Results indicated that a decrease from an average of 3.5 species per sample to 1.5 species per sample occurred with long-term exclosure. Along with a decrease in the number of species per sample, there was an increase in the percentage and weight of *Bromus* in the six-year exclosure. A large accumulation of litter in the exclosure was probably responsible for the changes observed. The few changes observed in the first-year exclosure were probably due to low population densities of *Microtus*. The results show that the removal of *Microtus* can and does cause significant changes in an old field community.

# INTRODUCTION

The hypothesis presented in this paper is that Microtus pennsylvanicus, by its presence and activities, 1) influences the species composition and diversity and 2) physiognomy, of an old field community.

A community has been defined as a "system of organisms living together and linked together by their effects on one another and their responses to the environment they share" (Whittaker, 1970). The manner in which populations of organisms interact with each other and with their environment to produce some resultant community-type is one of the fundamental questions with which ecologists have traditionally dealt.

The importance of animals in community dynamics has been investigated by a number of authors. Paine (1966) demonstrated that the starfish, Pisater spp., is an integral part of the intertidal community of the rocky Pacific seacoast. Through its predation upon the sessile invertebrates, Pisaster determines which species are present and also causes an increase in the number of species in the community. Cantlon (1969) discovered that the equilibrium of a particular forest ecosystem is dependent upon a small invertebrate predator of the parasitic plant, Melampyrum spp. Similar findings have been observed concerning herbivorous mammals.

Harper (1969) suggested that the predation upon vegetation by plant-eating mammals is very important in determining the vegetational diversity in any particular area. Studies conducted on rabbit populations in England reveal the importance of this animal in influencing the plant species which inhabit the various grassland communities (Tansley and Adamson, 1925; Hope-Simpson, 1940; Watt, 1962). Tansley and Adamson, for example, found that the absence of heavy grazing by rabbits allowed the invasion of plant species not characteristic of the community. Although much smaller herbivores than rabbits, voles have been shown to have a significant effect on community vegetation (Summerhayes, 1941; Batzli and Pitelka, 1970). According to Summerhayes, the removal of the vole, Microtus agrestis, caused a decrease in plant species other than the dominants. He attributed these effects to the tunnelling and feeding activities of the voles keeping the community open and, thereby, creating a habitat more favorable to the continued existence of a greater number of plant species.

The specific objective of the study was threefold: (1) to determine the effects of the exclusion of Microtus pennsylvanicus upon vegetational diversity, taxanomic composition, and physiognomy, (2) to measure the amount of plant biomass of the various species consumed by the vole population, and (3) to relate the above data to a mechanism by which these vegetational effects are maintained.

# DESCRIPTION OF THE STUDY AREA

The study was conducted on a grassy power line right-of-way approximately two miles south of the main campus of Michigan State University in Ingham County, Michigan. The field, approximately 0.5 hectares, is bordered on two sides by gravel roads beyond which are a woodlot and a cultivated area, respectively. A third side is bounded by a small woodlot and the fourth by an extension of the right-of-way. The field has lain relatively undisturbed since it was cleared of forest vegetation more than ten years before.

The field is gently undulating with a small depression at the west end that serves as a drain during the heavy rains in winter and spring. The soil on the study area is predominantly Conover.

The climate of the area is characterized by cold winters and mild summers. The mean annual temperature is 8.33 C with extreme ranges of -27.8 C to +43.33 C. The growing season is approximately 147 days. Yearly precipitation averages 78 cm with an average of 43 cm during the growing season (Baten and Eichmeier, 1951).

Perennial grasses dominate the vegetation of the area. The most conspicuous plant in the field is smooth brome grass, *Bromus inermis*, with Kentucky blue grass, *Poa pratensis*, and Canada blue grass, *P. compressa*, present to a lesser degree.

Isolated patches dominated by reed canary grass, *Phalaris arudinacea*, are scattered through the wetter portions of the field. A woody, shrub overstory consisting primarily of hawthorn, *Crataegus* spp., and raspberry, *Rubus occidentalis*, occurs sporadically over the field. The presence of numerous woody plants indicates a late stage of development of the grass-dominated old field seral stage. A total list of plant species sampled during the study can be found in Table 1.

Small mammals known to be present on the field are *Sorex cinereus*, *Blarina brevicauda*, *Peromyscus maniculatus*, *Microtus pennsylvanicus*, and *Zapus hudsonicus*.

TABLE 1. ALPHABETICAL LIST OF SAMPLED SPECIES

| | | |
|---|---|---|
| *Agropyron repens* | *Linaria vulgaris* | *Psedera quinquefolia* |
| *Bromus inermis* | *Phalaris arudinacea* | *Rhus radicans* |
| *Carex* spp. | *Phleum pratense* | *Smilacina stellata* |
| *Cirsium arvense* | *Plantago Rugeli* | *Solidago canadensis* |
| *Erythronium* sp. | *Poa compressa* | *Spiraea latifolia* |
| *Euonymus obovatus* | *P. pratensis* | *Taraxacum officinale* |
| *Geranium maculatum* | *Podophyllum pelatum* | *Viola* sp. |
| *Hypericum* sp. | *Potentilla recta* | *Vitis* sp. |

# METHODS

## Exclosure Experiment

Mouse-proof fences, designed for the selective exclusion of *Microtus pennsylvanicus*, enclosed two experimental plots on the study area. The first (hereafter called the six-year plot), erected in 1966, enclosed a 7 x 28 m area, which had been further subdivided into sixteen 3.5 x 3.5 m subplots. The second (hereafter called the first-year plot), constructed in May, 1971, just prior to the beginning of the study, enclosed an 8 x 16 m area with 4 x 4 m subplots.

Similar areas, but unfenced, directly adjacent to the experimental plots were designated as six-year and first-year control plots. Each control area was subdivided into the same number and size subplots as its fenced counterpart.

A diagramatic representation of the field experimental design is shown in Figure 1.

The fence surrounding each experimental area consisted of a bottom portion of ¼ inch mesh, hardware cloth extending about 45 cm both below and above ground levels. Contiguous with the hardware cloth was an upper portion of smooth aluminum sheeting raising the height of the fence to approximately 1 m. Extending the fence into the ground prevented the voles from burrowing beneath while the aluminum sheeting proved an equal deterrent to animals trying to climb the

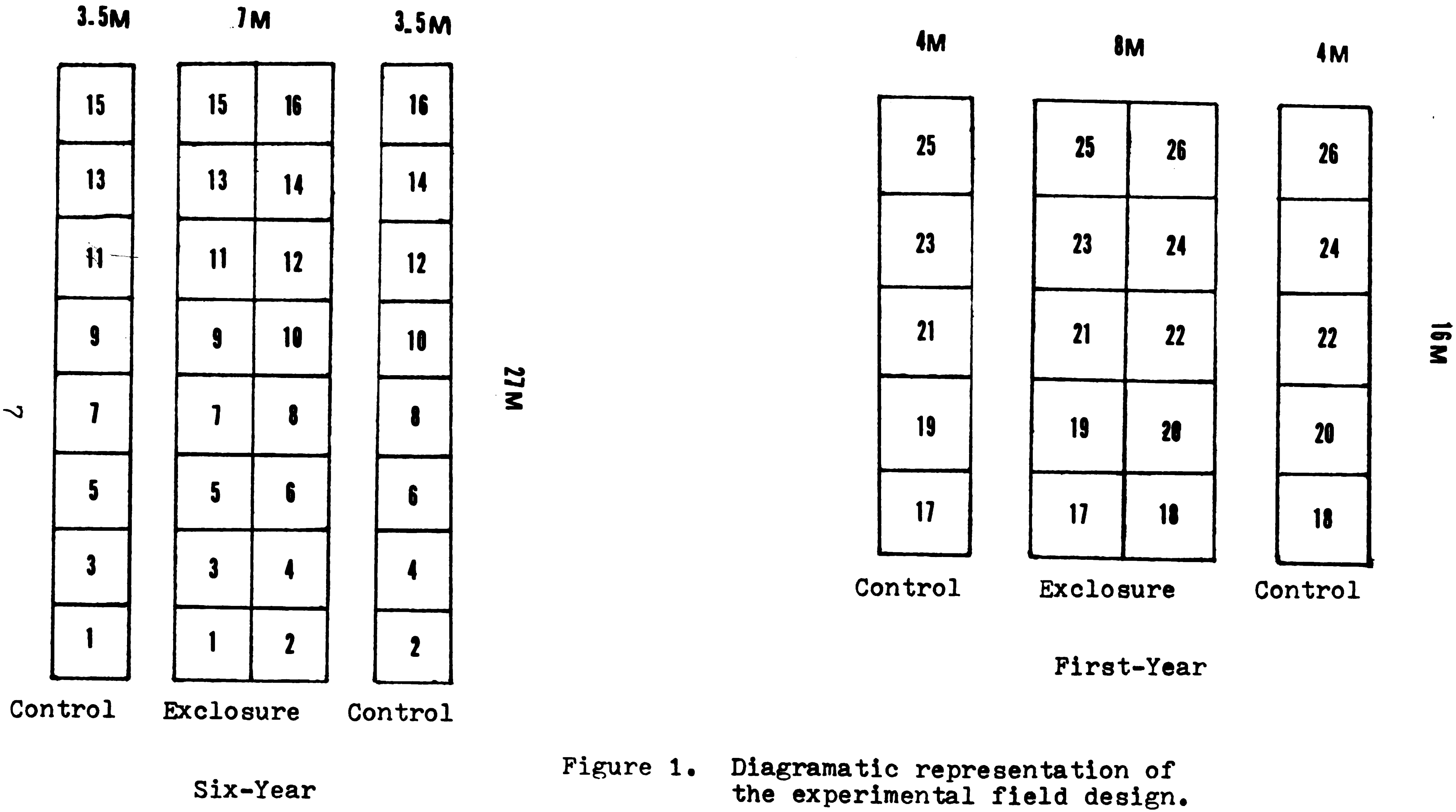


Figure 1. Diagramatic representation of the experimental field design.

fence. The mesh-size of the hardware cloth prevented voles from entering but allowed both soil and surface invertebrates free movement through the fence. In addition, movements of both _Zapus hudsonius_ and _Peromyscus maniculatus_, two important mammalian members of the community, were also not seemingly restricted by the presence of the fence since both species were often trapped in the exclosures.

All voles were trapped and removed from experimental areas prior to the study. The movements of voles onto the unfenced control areas were not restricted.

## Sampling of Vegetation

The sampling of vegetation was begun on May 15, 1971, and, with one exception, was conducted at three-week intervals until August 21. There were a total of six collection periods.

During each period of measurement, forty samples were collected, ten from each of the two experimental and control plots. Samples from the first collection period (May 15) were gathered from only the six-year plots, allowing the first-year plot a period of recovery from the disturbance caused by construction. Difficulties during the fourth measurement period (July 10) allowed for only five samples to be collected from the first-year control plot.

Each experimental plot was divided into two equal rows. Each row was separated into groups of three subplots in the six-year area and two groups of two subplots in the first-year plot. From each group of subplots, one was selected at random for use in sampling. A total of four subplots were sampled in each area. The same procedure was followed in unfenced control areas.

To remove any gradient differences inherent in the field, five of ten samples were collected from each row. In each row two samples were taken from one group and the remaining three samples were gathered from the second group. The 2-3 pattern from the first row was always reversed for the second.

Each subplot was divided into an eleven by eleven grid pattern. Each of the eleven points was approximately 25 cm apart. To take a sample, a pair of numbers was randomly selected and a line was drawn corresponding to each number. A frame was placed at the intersection of the two lines and the sample was collected.

A vegetative sample consisted of all plant material rooted within the confines of a 20 x 20 cm wire frame. Vegetation was clipped at ground level and, along with all enclosed litter, was marked and placed into plastic bags. All samples were refrigerated until a complete laboratory analysis could be completed.

## Analysis of Vegetation

Each refrigerated sample was divided into living plant and litter material. The height of each individual of the dominant brome grass was measured and recorded. Living vegetation was segregated as to species and dried in an oven at 100 C for twenty-four hours. The dry weight for each species, as well as for the litter material, was recorded for each sample.

## Trap Study

Small mammals were live trapped in order to determine location of the local populations, as well as to arrive at a relative density index of resident populations. Thirty Sherman live traps, baited with rolled oats, were placed in a grid pattern covering the 0.5 hectare field. The traps were placed 12 meters apart in six rows, each containing five traps. Traps were also placed into experimental areas in order to remove any voles entering the plots. Traps were set in late afternoon and checked the following morning. Trapping was conducted every four weeks for five days.

The captured animals were toe-clipped and released after recording the following data: species, location, number, sex, approximate age (based on size), and date of capture.

# RESULTS

## Plant Diversity and Composition

### Six-Year Plot

The mean number of species per sample for the ten samples collected during each sampling period was used as an index of species diversity of the sampled area. Means of the exclosure plots, with a range from 1.5 to 2.4 species per sample during the study, were lower than those of the adjacent controls. Control plots showed a range of 3.4 to 4.3 species per sample (Figure 2). Analysis of variance of the data indicated that the difference between control and exclosure plots was highly significant (*p* .001). Data for each sampling period are given in Table 2.

Analysis of biomass data for each sampling period indicates brome grass, *Bromus inermis*, to be dominant, i.e., it composes greater than fifty percent of the total standing crop, in both control and exclosure areas (Figure 3). Percentages in exclosure plots were higher than in control areas. Ranges were from 61.6% to 82.5% in control plots and 88.6% to 96.9% in exclosures (Table 3). A highly significant difference (*p* .001) between control and exclosure plots was indicated by an analysis of variance.

Time seemed to be a factor influencing the percentages of brome grass in sampled areas. Although no significant differences (p .10) existed between sampling periods, low percentages were recorded during the early stages of the study. Changes in brome grass percentages in control areas were probably due to the period of growth of this species. Since it is a late growing species, brome grass percentage was lowered by early growing species.

Along with a difference in the percentage of Bromus, there also existed a brome grass weight differential between control and exclosure plots (Figure 4). Mean weights of Bromus inermis ranged from 4.5 gms to 25.4 gms in exclosure areas and from 4.5 gms to 18.1 gms in adjacent control plots. Analysis of variance indicated the weight difference to be highly significant (p .005). The mean, standard error, and range for each sampling period can be found in Table 4.

## First-Year Plot

Values for the mean number of species per sample ranged from 2.6 to 3.9 species per sample in exclosure plots and 2.8 to 3.5 species per sample in adjacent control areas (Table 2a). There appeared to be little difference between the two areas (Figure 2a) and the difference was not significant (p .05).

Brome grass, with one exception, composed greater than fifty percent of the total plant standing crop in both control and exclosure plots and from 68.9% to 83.1% in control areas (Table 3a). Percentages appeared higher in control areas than in exclosure plots (Figure 3). A significant difference (p .025) existed between the two plots. Time also influenced the percentage of brome grass but this value was not significant.

The mean weight of brome grass per sample ranged from 5.2 gms to 16.4 gms in exclosure plots and from 5.4 gms to 16.1 gms in controls (Table 4a). There was no difference (p .75) between the weight of brome grass in control and exclosure plots (Figure 4a).

## Plant Biomass

### Six-Year Plot

The mean biomass (gms/$m^2$) per sample, i.e., standing crop, of vegetation for each measurement period's ten samples, ranged from 133.3 to 670.8 g/$m^2$ in the exclosure plots and from 174.3 to 538.5 g/$m^2$ in adjacent control plots (Table 5). Both areas showed a steady increase (Figure 5) in biomass until a peak was reached at the fifth sampling period (July 31). This peak was followed by a decrease at the last period (August 21). The decrease was due to the dying of many of the early flowering species. The exclosure plots reached a higher peak than the control plots but this difference was not significant.

Mean weights of litter material (dead plants) were greater in exclosure plots (Figure 6). The range in the exclosure plots was from 31 g to 39.5 g and appeared to be composed primarily of <u>Bromus inermis</u>. This letter formed a dense mat about six inches above soil level. Litter in control plots was of mixed species composition. Mean weights per plot ranged from 22.9 g to 27.4 g (Table 6). The mat seen in exclosure areas was absent in control plots. The difference in weight between the two areas was highly significant (p .001).

Litter in both exclosure and control plots showed an initial decrease in the amount during the first three sampling periods. Throughout the remainder of the study, an increase in the mean weight was observed as early season plants began dying.

## First-Year Plot

Little difference was observed in the standing crop between control and exclosure plots. A lower standing crop in control plots, which was at first thought to be an indication of the total amount removed by *Microtus* grazing, during the initial sampling periods was later reversed showing a greater biomass than in exclosure plots (Figure 5). The range in the exclosure plots was from 325.8 to 538.5 $g/m^2$ and from 198 to 524 $g/m^2$ in control plots (Table 5a). Differences in the total standing crop between the two areas were not significant.

The mean weight of litter in both exclosure and control plots appeared almost identical throughout most of the study. The only exception occurred during the fourth sampling period (Figure 6a) when the increase in control litter was due to the smaller sample size taken primarily from an area usually high in the amount of litter. Ranges were from 20 to 25.2 g in the exclosure plots and from 20.7 to 29.1 g in the control plots (Table 6b). The difference between the two areas was not significant. As in the six-year experiment, litter weights increased toward the end of the study due to the dying of early flowering species.

According to Thompson (1965), *Poa* spp. ranks high on the list of preferred foods of *Microtus*. Of those foods which

Thompson lists as most preferred, Poa spp. is the only one present with any degree of abundance in the study plots. For this reason, weights of Poa were recorded for both control and exclosure plots to determine the amounts removed by the grazing of the vole population. Mean weights were greater for exclosure plots throughout most of the study (Figure 7). Means ranged from 1.8 g to 3.7 g in exclosure plots and from 1.5 g to 2.7 g in control plots (Table 7). The difference between the two areas was not significant (p .10) as indicated by analysis of variance. High weights during the early part of the study and a decrease as time progressed indicate that this grass is an early growing season species.

## Community Physiognomy

### Six-Year Plot

A change in plant growth form occurred in the exclosure plots. Whereas, the control area was typical of most old field communities; that is, a mixed grass-forb community, the exclosure plot consisted almost entirely of grasses as shown by the high percentage of Bromus inermis (about 95%). Non-graminoid plant species were not an important aspect of the exclosure community.

The density (mean number individuals per sample) of Bromus inermis showed a tendency throughout the entire study to be greater in the exclosure plots than in the controls (Figure 8). This difference in density was indicated by the analysis of variance to be significant (p .025). Mean densities ranged from 21.4 to 29.2 in exclosure plots and from

15.2 to 23.3 in control plots (Table 8). As a result of the increased dencity, the exclosures looked more productive. Vegetation appeared more lush and the area more filled with plant material. Control areas appeared to be more open, with less plant cover than the exclosure areas.

Measurements of the dominant brome grass indicated that the grass height, early in the season, was less in the exclosure plots but reached a higher peak in this area than in the control plots. A decrease in mean grass height in control plots (Figure 9) at the end of the study was caused by a substantial secondary growth which had begun to appear. Means for exclosure plots ranged from a minimum of 272.3 mm during the first sampling period (July 31) to a maximum of 696.5 mm during the fifth period. Control plots had a minimum of 327.5 mm during the first period but had a maximum of 642.7mm during the fourth period (Table 9). It was during the fourth period that the secondary growth previously mentioned first appeared. The difference between the heights of the two areas was not statistically significant.

## First-Year Plot

Growth-forms for both control and exclosure plots were identical. Each community was of the usual old field type. Each was composed of both graminoids and forb plant species. In both areas the total plant cover consisted of greater than 90% grasses.

The density of _Bromus inermis_ was variable for the two plots. No trends were clearly visible for the two areas

(Figure 8). Means varied from 15.1 to 23.5 individuals per sample in the exclosure plots and from 18.7 to 24.8 in control plots (Table 8a). Differences between the two areas were not statistically significant.

Height measurements indicated little difference between control and exclosure plots (Figure 9). The range of means was from 416.4 mm to 648 mm in exclosure plots and from 384.6 mm to 611.1 mm in control plots (Table 9a). A decrease in height from the third to fourth sampling periods in control plots was probably due to the smaller sample size in the fourth period.

## Species-Litter Interaction

In the six-year exclosure experiment the mean number of species per sample was plotted versus the mean weight of litter per sample (Figure 10). A correlation coefficient of -.90 was obtained for these two values.

## Trapping Results

Indications from trap periods were that the population of Microtus was at a low density level. Results were not good enough to be able to give any significant estimates, but it was apparent that numbers were low. Because of the large number of juveniles that appeared in traps, it is assumed that the vole population was in an increasing phase of growth.

During the early stages of the study, voles were not found on the study area proper. Instead, the population was found confined to an area of the field surrounding a drainage ditch. As conditions changed during the late spring, the vole population moved onto the study area where they remained throughout the rest of the study.

Table 2. Mean, standard error, and range of number of species per sample from six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard Error | Range | F value |
|---|---|---|---|---|---|
| 1 | exc. | 1.5 | 0.269 | 1-3 | 73.79 |
| 1 | con. | 4.0 | 0.394 | 2-6 | |
| 2 | exc. | 2.1 | 0.348 | 1-4 | |
| 2 | con. | 3.8 | 0.327 | 2-5 | |
| 3 | exc. | 2.4 | 0.427 | 1-5 | |
| 3 | con. | 3.4 | 0.340 | 1-5 | |
| 4 | exc. | 1.8 | 0.291 | 1-4 | |
| 4 | con. | 4.3 | 0.496 | 1-6 | |
| 5 | exc. | 2.4 | 0.271 | 1-5 | |
| 5 | con. | 3.6 | 0.452 | 1-5 | |
| 6 | exc. | 1.8 | 0.248 | 1-3 | |
| 6 | con. | 4.1 | 0.458 | 2-7 | |

Table 2a. Mean, standard error, and range of number of species per sample from first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard Error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 3.8 | 0.291 | 3-5 | 0.45 |
| 2 | con. | 2.8 | 0.291 | 2-5 | |
| 3 | exc. | 3.2 | 0.327 | 2-5 | |
| 3 | con. | 3.3 | 0.448 | 1-6 | |
| 4 | exc. | 3.9 | 0.407 | 2-6 | |
| 4 | con. | 3.2 | 0.583 | 2-4 | |
| 5 | exc. | 2.9 | 0.406 | 2-6 | |
| 5 | con. | 3.5 | 0.500 | 1-7 | |
| 6 | exc. | 2.6 | 0.339 | 1-5 | |
| 6 | con. | 2.8 | 0.325 | 1-4 | |

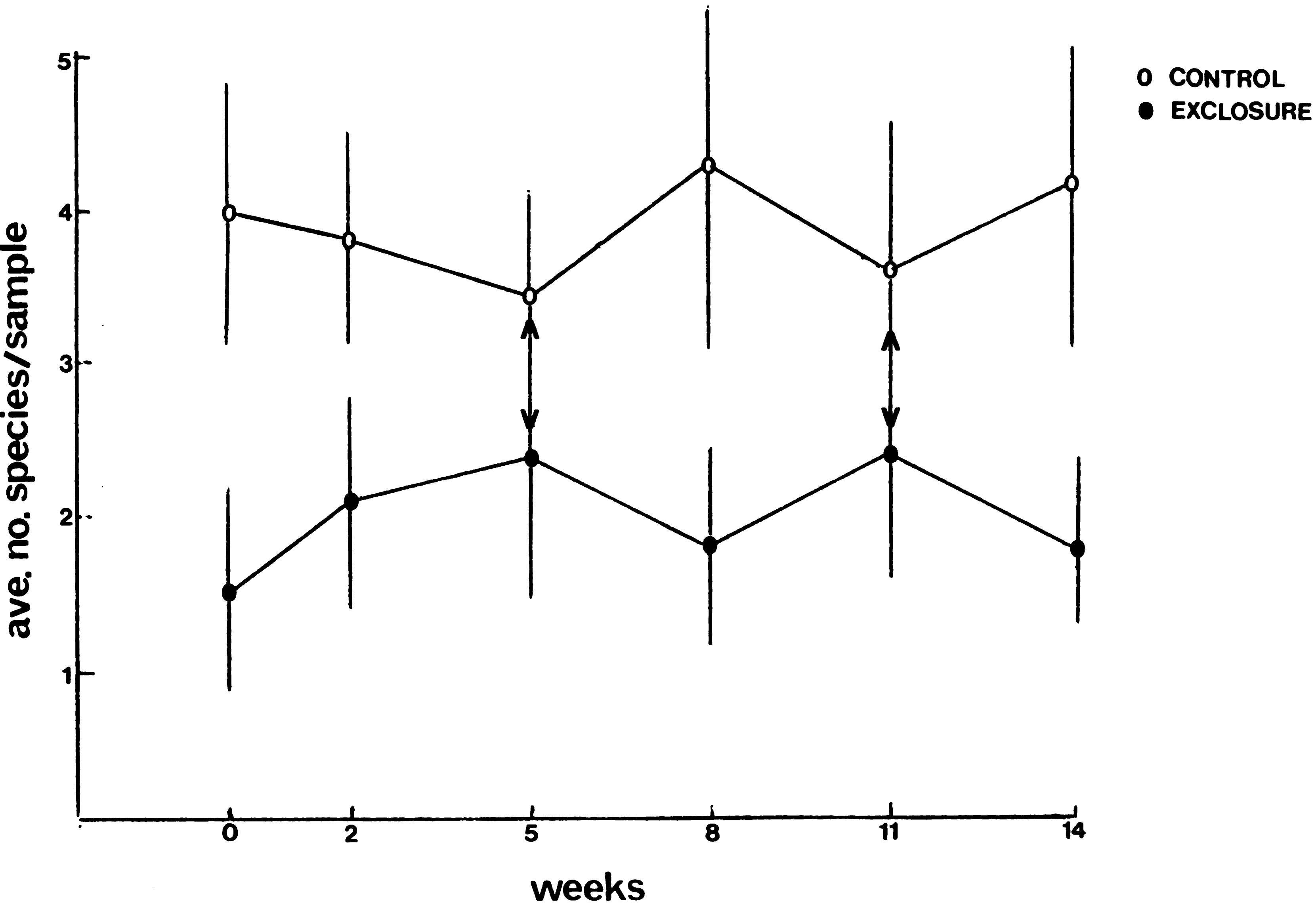


Figure 2. Mean number of plant species per plot with associated 95% confidence limits for each sampling period of the six-year exclosure experiment.

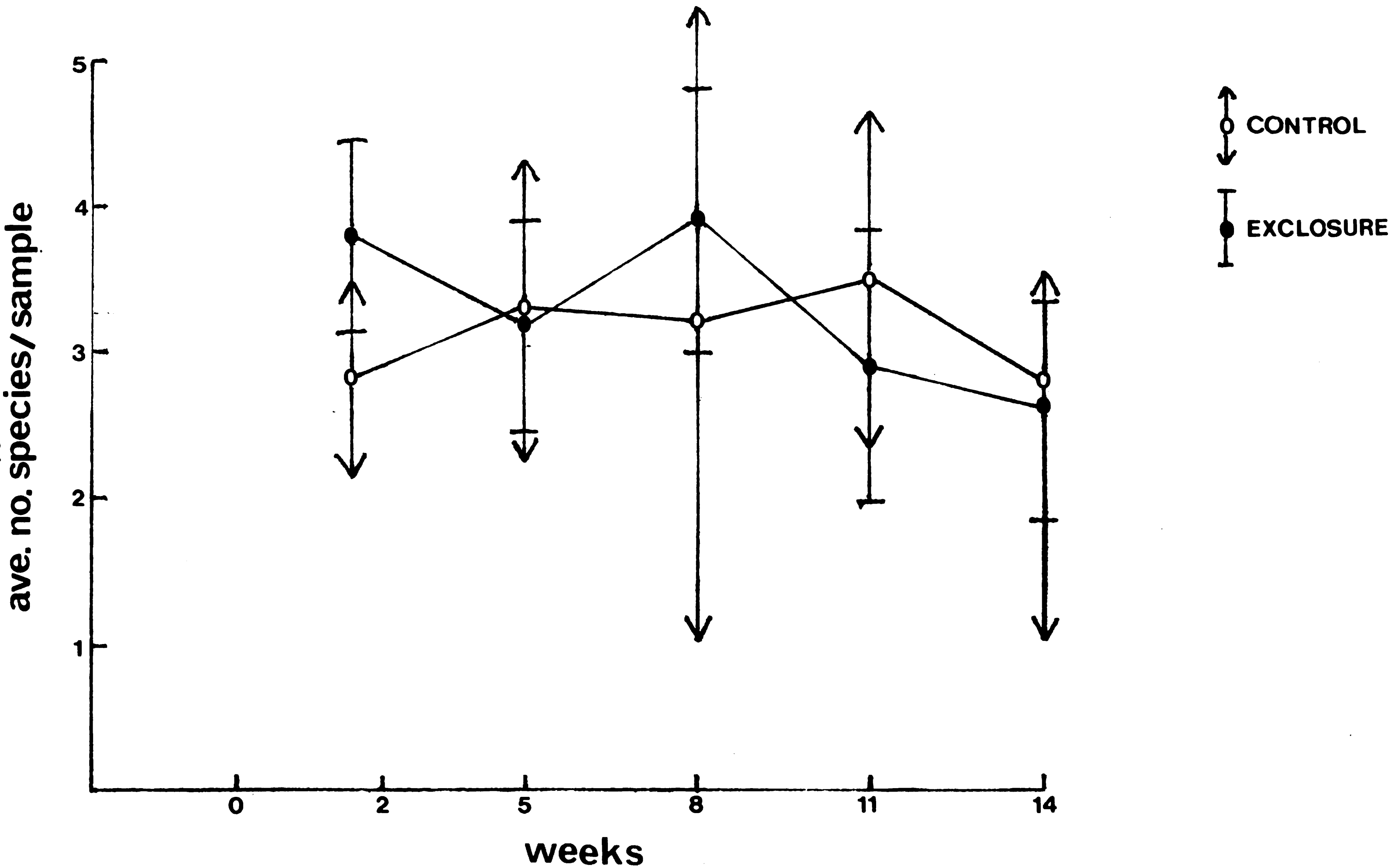


Figure 2a. Mean number of plant species per plot with associated 95% confidence limits for each sampling period of the first-year exclosure experiment.

Table 3. Mean, standard error, range, and F value for the percentage of the total standing crop of *Bromus inermis* for the six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 1 | exc. | 88.7 | 6.60 | 37.8-100 | 58.37 |
| 1 | con. | 61.2 | 7.76 | 20.9-97.2 | |
| 2 | exc. | 92.5 | 3.71 | 63.1-100 | |
| 2 | con. | 67.7 | 3.55 | 51.6-85.7 | |
| 3 | exc. | 93.5 | 2.54 | 77.0-100 | |
| 3 | con. | 81.7 | 4.11 | 58.6-100 | |
| 4 | exc. | 96.9 | 1.22 | 88.6-100 | |
| 4 | con. | 71.1 | 6.05 | 33.5-100 | |
| 5 | exc. | 93.9 | 1.61 | 85.2-100 | |
| 5 | con. | 82.5 | 4.83 | 55.3-100 | |
| 6 | exc. | 96.0 | 2.61 | 73.0-100 | |
| 6 | con. | 80.9 | 5.23 | 56.0-99.4 | |

Table 3a. Mean, standard error, range, and F value for the percentage of the total standing crop of *Bromus inermis* for the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 44.8 | 6.61 | 14.5-85.7 | 5.[illegible]5 |
| 2 | con. | 68.9 | 4.32 | [illegible]5.1-92.[illegible] | |
| 3 | exc. | 69.6 | 9.98 | 0[illegible]-99 | |
| 3 | con. | 81.2 | 5.17 | 49.3-100 | |
| 4 | exc. | 64.0 | 7.42 | 14.4-86.5 | |
| 4 | con. | 78.4 | 7.76 | 54.2-94.4 | |
| 5 | exc. | 78.2 | 7.09 | 22.9-98.5 | |
| 5 | con. | 69.0 | 9.50 | 3.20-100 | |
| 6 | exc. | 68.4 | 9.09 | 53.6-100 | |
| 6 | con. | 83.1 | 4.97 | 10.3-100 | |

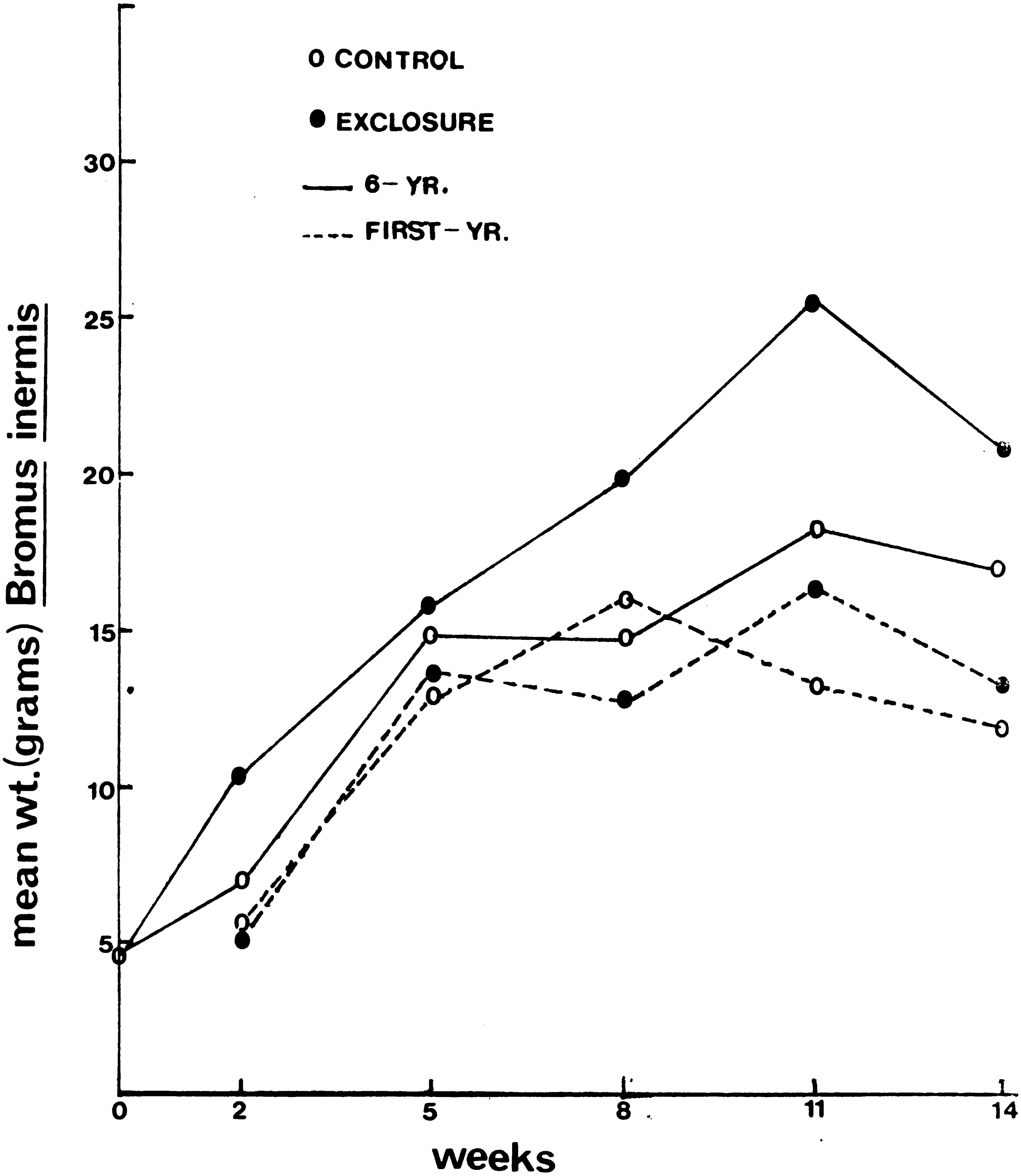


Figure 3. Mean weight (grams) of Bromus inermis per sample for each sampling period of the two exclosure experiments.

Table 4. Mean, standard error, range, and F value of the weight of <u>Bromus inermis</u> from the six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 1 | exc. | 4.5 | 0.59 | 1.6-8.2 | 9.07 |
| 1 | con. | 4.5 | 0.89 | 0.9-10.5 | |
| 2 | exc. | 10.4 | 1.47 | 4.6-18.4 | |
| 2 | con. | 7.0 | 0.85 | 4.2-12.8 | |
| 3 | exc. | 15.8 | 2.80 | 6.6-33.2 | |
| 3 | con. | 14.8 | 2.08 | 3.6-23.6 | |
| 4 | exc. | 19.7 | 2.10 | 12.3-34.7 | |
| 4 | con. | 14.8 | 2.95 | 5.4-38.2 | |
| 5 | exc. | 25.4 | 2.04 | 14.4-35.2 | |
| 5 | con. | 18.1 | 1.93 | 6.7-27 | |
| 6 | exc. | 21.7 | 2.73 | 9.5-36.5 | |
| 6 | con. | 16.9 | 2.82 | 6.7-25.6 | |

Table 4a. Mean, standard error, range, and F value of the weight of <u>Bromus inermis</u> from the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 5.2 | 0.85 | 2.6-10.8 | 0.05 |
| 2 | con. | 5.4 | 0.90 | 2.3-12.2 | |
| 3 | exc. | 13.7 | 2.37 | 0 -26.5 | |
| 3 | con. | 13.2 | 1.65 | 5.9-23.2 | |
| 4 | exc. | 12.9 | 1.54 | 2.7-19.3 | |
| 4 | con. | 16.1 | 2.32 | 9.6-22.1 | |
| 5 | exc. | 16.4 | 2.65 | 3.4-26.7 | |
| 5 | con. | 13.3 | 2.80 | 0.4-29.1 | |
| 6 | exc. | 13.2 | 1.77 | 5.1-23.8 | |
| 6 | con. | 12.0 | 2.51 | 2.4-28.8 | |

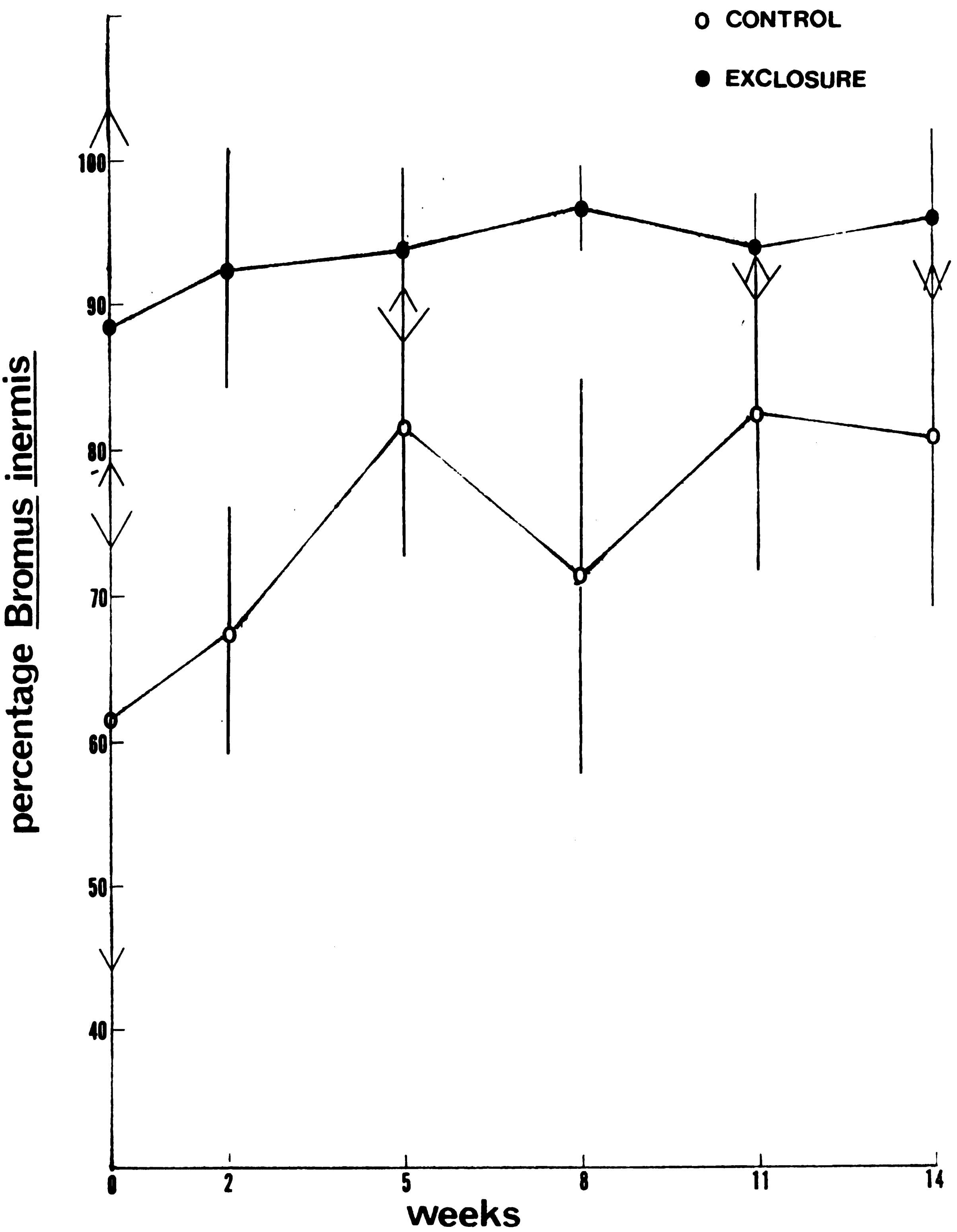


Figure 4. Mean percentage of <u>Bromus inermis</u> per sample with associated 95% confidence limits for each sampling period of the six-year exclosure experiment.

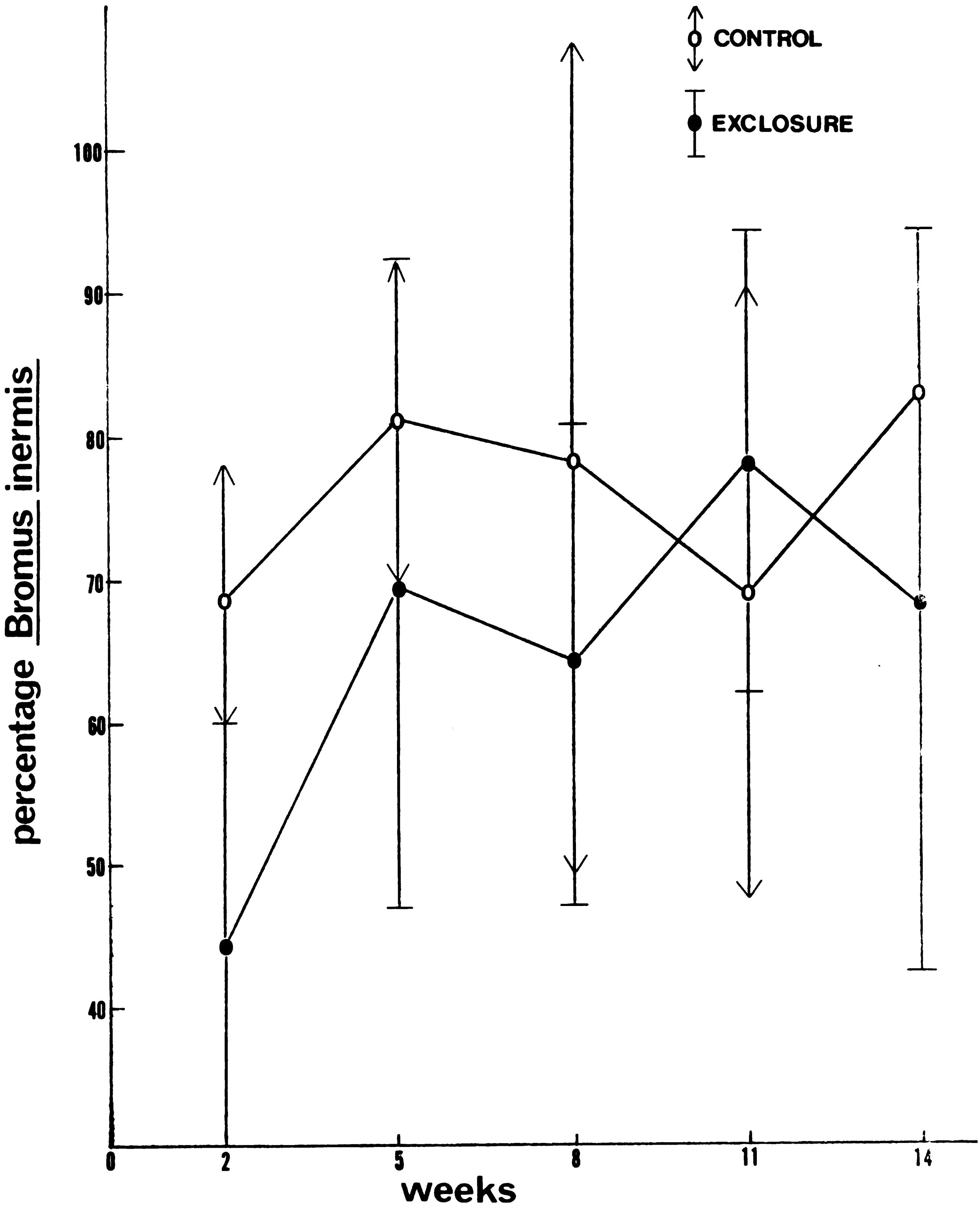


Figure 4a. Mean percentage of Bromus inermis per sample with associated 95% confidence for each sampling period of the first-year exclosure experiment.

Table 5. Mean, standard error, range, and F value of the standing crop (gms.m.$^2$) of the vegetation from the six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 1 | exc. | 133.3 | 19.71 | 40 -262.5 | 0.72 |
| 1 | con. | 174.3 | 19.69 | 90 -290 | |
| 2 | exc. | 277 | 33.58 | 120 -460 | |
| 2 | con. | 259.5 | 27.51 | 122.5-405 | |
| 3 | exc. | 417.5 | 67.78 | 180 -830 | |
| 3 | con. | 438 | 48.81 | 130 -642.5 | |
| 4 | exc. | 506.5 | 51.07 | 315 -867.5 | |
| 4 | con. | 499 | 63.75 | 205 -955 | |
| 5 | exc. | 670.8 | 47.58 | 422.5-912.5 | |
| 5 | con. | 538.5 | 45.5 | 302.5-787.5 | |
| 6 | exc. | 560 | 66.52 | 302.5-922.5 | |
| 6 | con. | 507.3 | 52.9 | 265 -740 | |

Table 5a. Mean, standard error, range, and F value of the standing crop (gms./m.$^2$) of the vegetation from the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 325.8 | 48.23 | 155 -655 | 0.34 |
| 2 | con. | 198 | 31.19 | 102.5-442.5 | |
| 3 | exc. | 451.5 | 58.1 | 110 -832.5 | |
| 3 | con. | 403.3 | 37.9 | 167.5-580 | |
| 4 | exc. | 518 | 44.31 | 260 -725 | |
| 4 | con. | 505.5 | 24.51 | 442.5-615 | |
| 5 | exc. | 497.5 | 54.69 | 217.5-752.5 | |
| 5 | con. | 524 | 61.03 | 305 -850 | |
| 6 | exc. | 386.5 | 39.4 | 237.5-645 | |
| 6 | con. | 428.8 | 45.58 | 282.5-742.5 | |

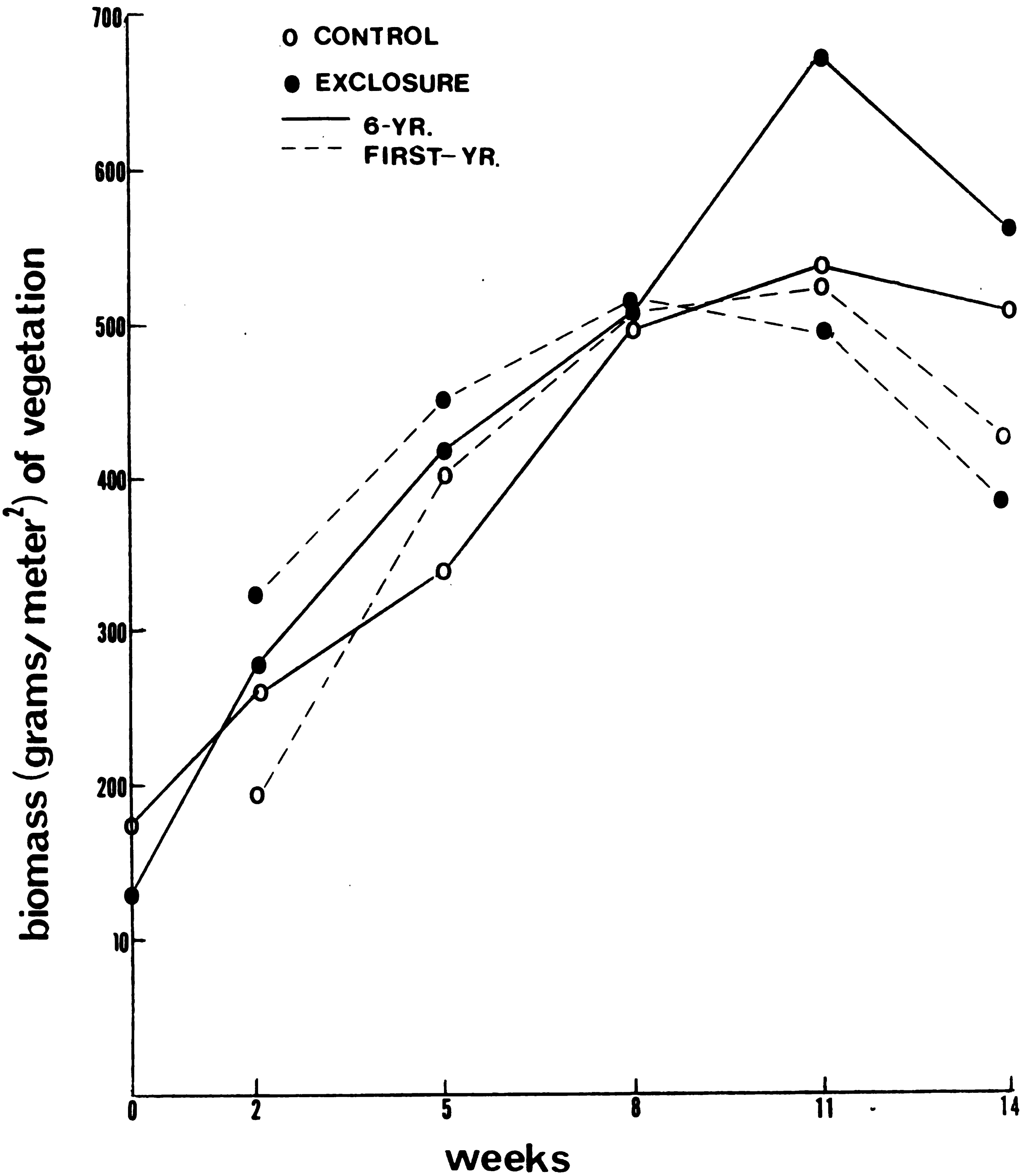


Figure 5. Mean standing crop (grams/meter$^2$) per sample for each sampling period of the two exclosure experiments

Table 6. Mean, standard error, range, and F value of the weight of litter material from the six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 1 | exc. | 39.5 | 3.32 | 23.8-62.7 | 64.16 |
| 1 | con. | 23.8 | 2.28 | 13.3-38.3 | |
| 2 | exc. | 37.4 | 3.19 | 19.1-52.5 | |
| 2 | con. | 23 | 1.23 | 18 -27.8 | |
| 3 | exc. | 30.9 | 2.68 | 23.3-49 | |
| 3 | con. | 22.9 | 1.37 | 15 -31 | |
| 4 | exc. | 34.3 | 2.16 | 26.8-44.7 | |
| 4 | con. | 26.7 | 2.23 | 16.6-41 | |
| 5 | exc. | 36.4 | 2.43 | 26 -48.4 | |
| 5 | con. | 27.4 | 2.29 | 16.9-41.4 | |
| 6 | exc. | 36.9 | 2.04 | 27.5-49.4 | |
| 6 | con. | 26.2 | 1.88 | 17.3-33.8 | |

Table 6a. Mean, standard error, range, and F value of the weight of litter material from the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 20 | 1.58 | 10.9-26.4 | 3.54 |
| 2 | con. | 20.7 | 0.99 | 16.2-26.4 | |
| 3 | exc. | 21.9 | 1.44 | 16.3-30.8 | |
| 3 | con. | 20.7 | 2.28 | 9.1-31 | |
| 4 | exc. | 20.6 | 1.85 | 13.7-32.5 | |
| 4 | con. | 29.1 | 4.34 | 13.5-40.4 | |
| 5 | exc. | 25.2 | 1.56 | 17.9-32.9 | |
| 5 | con. | 25 | 4.59 | 7.5-59 | |
| 6 | exc. | 24 | 1.87 | 17.5-33.8 | |
| 6 | con. | 23.3 | 2.18 | 13.6-36.3 | |

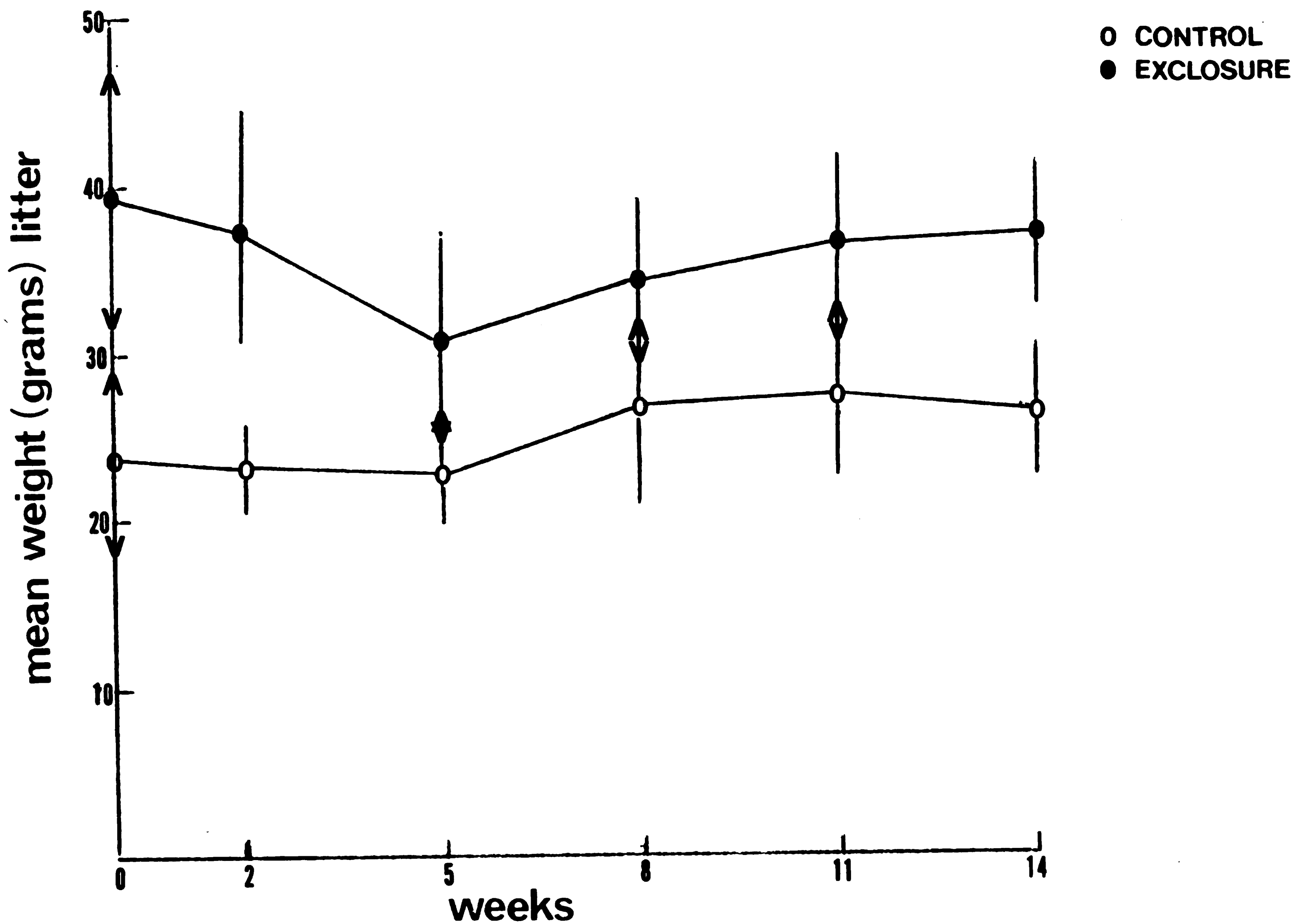


Figure 6. Mean litter weight per sample with associated 95% confidence limits for each sampling period of the six-year exclosure experiment.

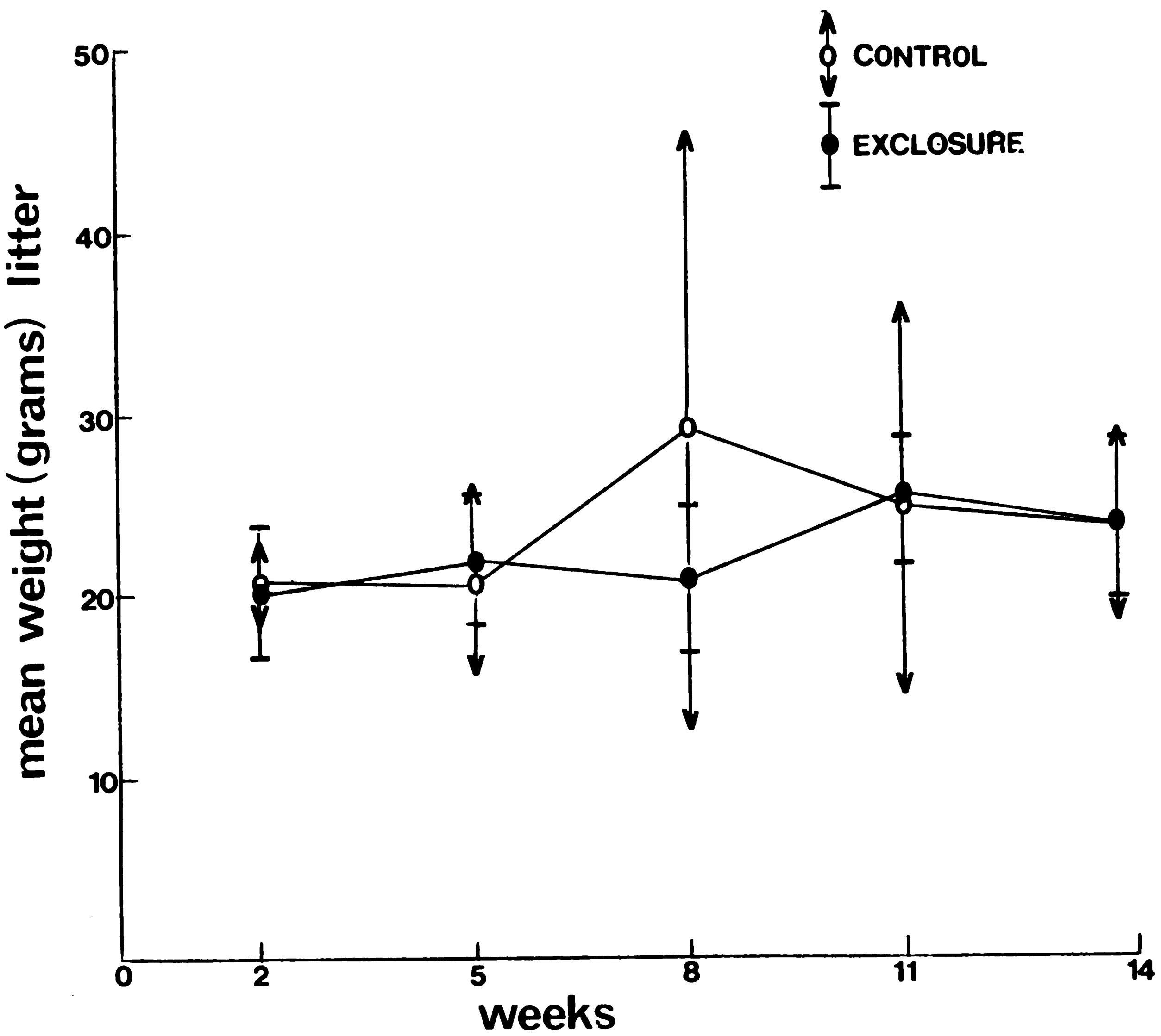


Figure 6a. Mean litter weight per sample with associated 95% confidence limits for each sampling period of the first-year exclosure experiment.

Table 7. Mean, standard error, range, and F value of the average weight of <u>Poa</u> spp. per sample from the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 3.5 | 0.53 | 1.1- 6.7 | 1.78 |
| 2 | con. | 1.9 | 0.35 | 0 - 3.9 | |
| 3 | exc. | 2.5 | 0.72 | 0 - 7.8 | |
| 3 | con. | 1.5 | 0.89 | 0 - 8.4 | |
| 4 | exc. | 3.7 | 0.77 | 0.9- 9.4 | |
| 4 | con. | 2.7 | 1.38 | 0 - 6.2 | |
| 5 | exc. | 2.9 | 1.06 | 0 -10.9 | |
| 5 | con. | 1.6 | 0.42 | 0 - 4.1 | |
| 6 | exc. | 1.8 | 0.46 | 0 - 4.4 | |
| 6 | con. | 2.4 | 0.72 | 0 - 6.4 | |

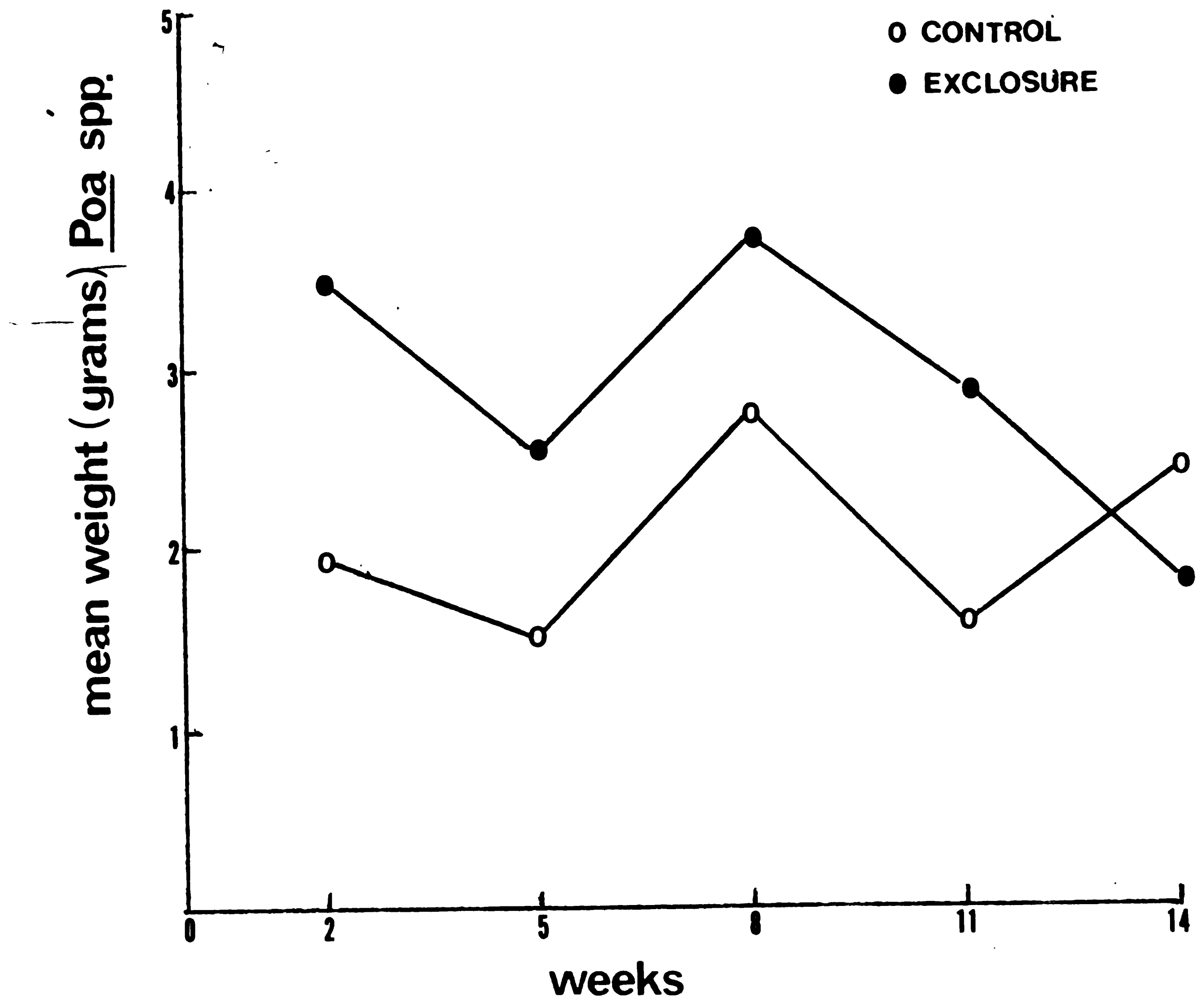


Figure 7. Mean weight (grams) of *Poa* spp. per sample for each sampling period of the first-year exclosure experiment.

Table 8. Mean, standard error, range, and F value of the mean density of *Bromus inermis* per sample from the six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 1 | exc. | 24.7 | 2.98 | 10-38 | 5.96 |
| 1 | con. | 23 | 3.56 | 10-30 | |
| 2 | exc. | 27.5 | 2.85 | 14-42 | |
| 2 | con. | 22 | 2.86 | 11-39 | |
| 3 | exc. | 21.4 | 2.13 | 14-33 | |
| 3 | con. | 21.3 | 2.79 | 7-37 | |
| 4 | exc. | 22.8 | 1.48 | 14-28 | |
| 4 | con. | 15.2 | 3.19 | 0-31 | |
| 5 | exc. | 29.2 | 1.96 | 21-39 | |
| 5 | con. | 23.3 | 2.90 | 10-38 | |
| 6 | exc. | 25.5 | 2.59 | 14-38 | |
| 6 | con. | 22.8 | 3.36 | 8-39 | |

Table 8a. Mean, standard error, range, and F value of the mean density of *Bromus inermis* per sample from the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Mean | Standard error | Range | F value |
|---|---|---|---|---|---|
| 2 | exc. | 17.6 | 3.11 | 5-31 | 1.09 |
| 2 | con. | 18.8 | 3.28 | 7-44 | |
| 3 | exc. | 21.8 | 2.96 | 10-39 | |
| 3 | con. | 24.8 | 2.97 | 9-44 | |
| 4 | exc. | 15.1 | 1.83 | 7-26 | |
| 4 | con. | 22.4 | 2.29 | 14-28 | |
| 5 | exc. | 23.5 | 3.23 | 5-36 | |
| 5 | con. | 19.6 | 3.73 | 1-37 | |
| 6 | exc. | 19.4 | 2.08 | 9-28 | |
| 6 | con. | 18.7 | 3.77 | 3-41 | |

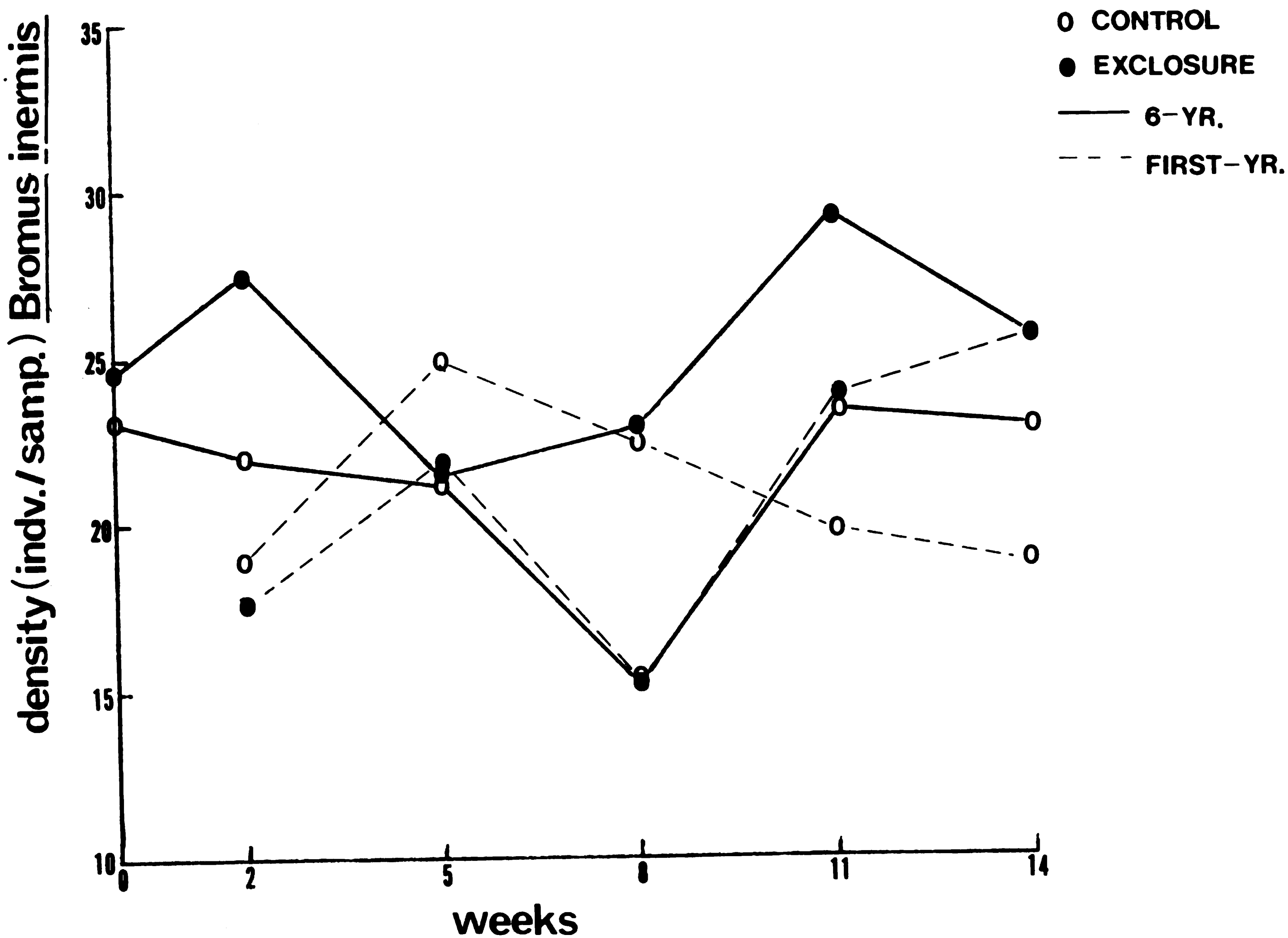


Figure 8. Mean density per sample of Bromus inermis for each sampling period of the two exclosure experiments.

Table 9. Mean, sample size, standard error, and F value of the average height (mm.) of Bromus inermis per sampling period from the six-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Sample size | Mean | Standard error | F value |
|---|---|---|---|---|---|
| 1 | exc. | 248 | 272.3 | 4.12 | 0.64 |
| 1 | con. | 230 | 327.5 | 3.88 | |
| 2 | exc. | 277 | 401.2 | 6.23 | |
| 2 | con. | 219 | 380 | 5.78 | |
| 3 | exc. | 214 | 721.9 | 15.30 | |
| 3 | con. | 213 | 652.3 | 11.61 | |
| 4 | exc. | 228 | 723.9 | 11.61 | |
| 4 | con. | 152 | 696.5 | 17.45 | |
| 5 | exc. | 292 | 731.1 | 11.21 | |
| 5 | con. | 232 | 642.7 | 15.47 | |
| 6 | exc. | 255 | 716.1 | 12.16 | |
| 6 | con. | 227 | 624.2 | 13.20 | |

Table 9a. Mean, sample size, standard error, and F value of the average height (mm.) of Bromus inermis per sampling period from the first-year exclosure (exc.) and control (con.) plots.

| Sampling period | Area | Sample size | Mean | Standard error | F value |
|---|---|---|---|---|---|
| 2 | exc. | 176 | 416.4 | 6.91 | 1.78 |
| 2 | con. | 188 | 384.6 | 6.79 | |
| 3 | exc. | 218 | 625 | 11.97 | |
| 3 | con. | 248 | 609.7 | 10.46 | |
| 4 | exc. | 151 | 648.4 | 16.31 | |
| 4 | con. | 113 | 560.3 | 19.06 | |
| 5 | exc. | 235 | 629 | 12.22 | |
| 5 | con. | 196 | 611.1 | 14.78 | |
| 6 | exc. | 194 | 635.3 | 15.79 | |
| 6 | con. | 187 | 609.5 | 13.56 | |

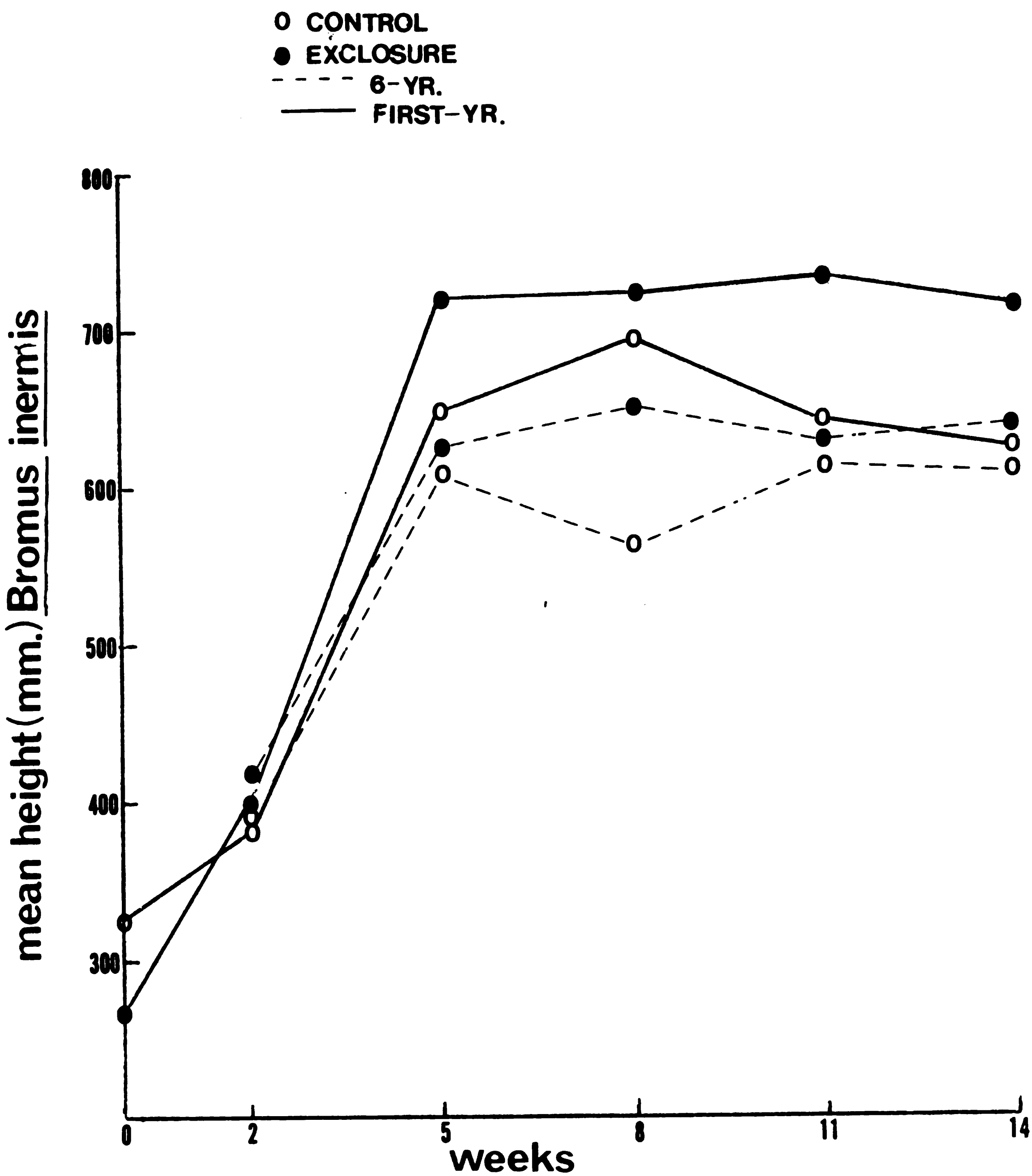


Figure 9. Mean height of Bromus inermis for each sampling period of the two exclosure experiments.

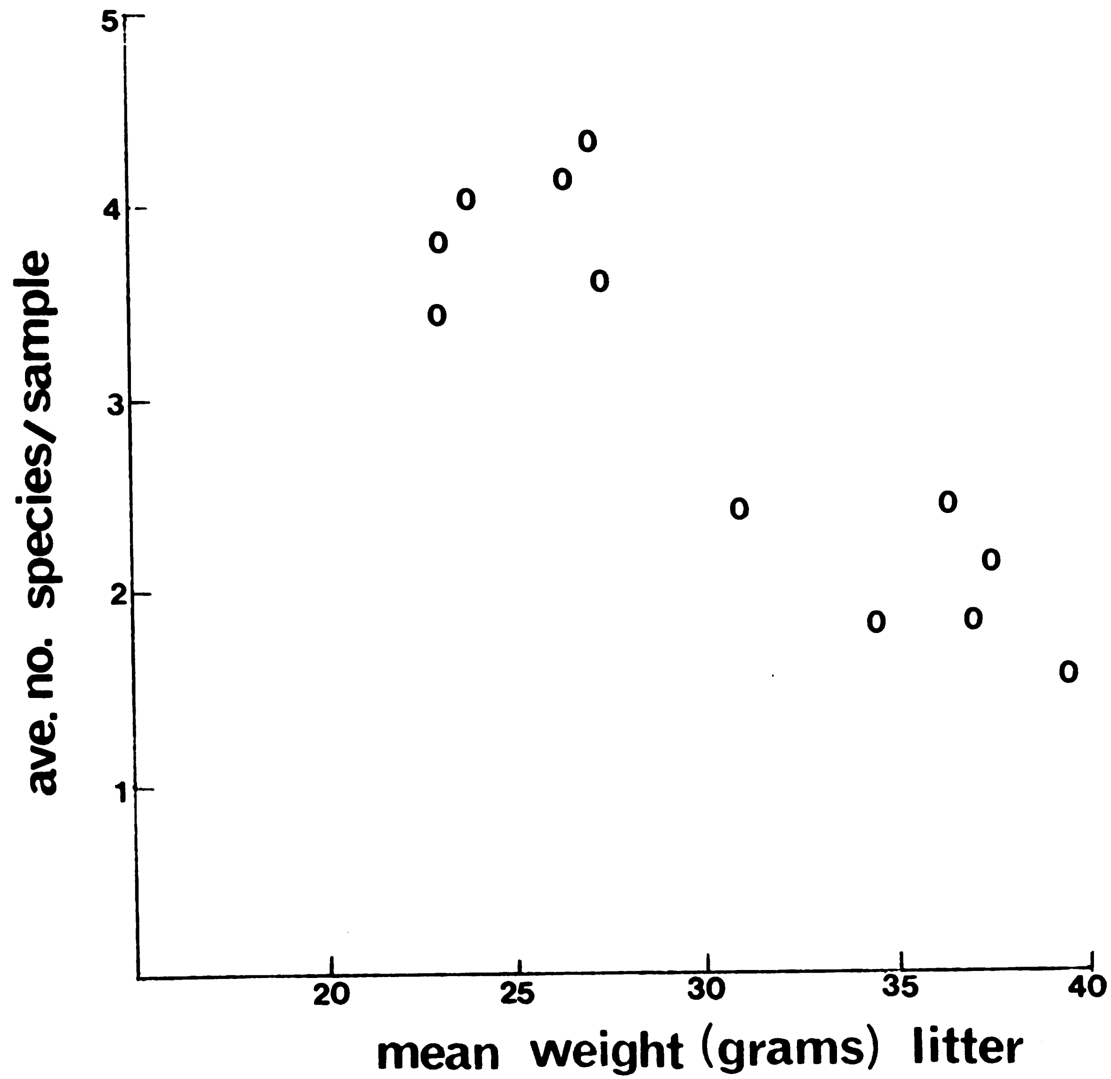


Figure 10. The mean number of species per sample versus the mean weight (grams) of litter for the six-year exclosure experiment. Correlation coefficient of -0.9 was obtained.

## DISCUSSION

The presence of *Microtus pennsylvanicus* caused an increase in the number of plant species inhabiting the old field community. With the removal of this important grazer, there was a decrease in the number of plant species found in the six-year exclosure plots. Similar decreases in community species diversity were found by several other investigators (Tansley and Adamson, 1925; Summerhayes, 1941; Paine, 1966; Harper, 1969) following the removal of other species of animals.

The decrease in the number of plant species was accompanied by an increase in the degree of dominance, represented by the percentage of the total standing crop of the dominant grass, *Bromus inermis*. Summerhayes (1944) reported a similar increase in the grass dominant following the removal of the vole, *Microtus agrestis*, in England.

The manner in which *Microtus* is able to maintain its influence is in the prevention of an excess accumulation of dead plant material. A dense mat of litter, as seen in the six-year exclosure, has been reported to be an important factor regulating the plant species composition and rate of growth (Heady, 1956). Weaver and Fitzpatrick (1934), Weaver and Bruner)1950), Sampson (1952), Weaver and Rowland (1952) discovered that the dominant plant maintains its purest stands in areas where an excess amount of litter has accumulated. Odum (1970) stated that such effects could be due to a disruption in mineral cycling, but in this case, it is more probable that changes in the microenvironment are the reason for the changes of species composition of the community. Weaver and Fitzpatrick (1934) and Weaver and Rowland (1952) determined that lower soil temperature under the litter accumulation delayed growth about three weeks in the situations that they studied. With the delay in growth, Weaver and Fitzpatrick found early species to be greatly handicapped and tended to disappear. The height of the mat would determine the presence or absence of the smaller plant species. In the case of the six-year exclosure, the litter mat extended from 6 to 12 inches above the ground. Species smaller than this would not be present due to an absence of sunlight. A combination of these factors caused the change from a mixed grass-forb community to a totally grass dominated one.

The delay in growth would explain the smaller grass height in the six-year exclosure at the beginning of this study. Weaver and Fitzpatrick (1934) noted that the litter would retard growth in the spring. As the soil warmed and the grass pierced the mat, the height was able to surpass the height of the grass in the control plots.

The manner in which <u>Microtus</u> is able to reduce the litter mat is not understood. Summerhayes (1941) claimed that the effect was related to the run-way building activity, characteristic of this species of vole. While this is a distinct possibility, it is also probable that activity under the snow during the winter could be very important. <u>Bromus</u> remains green above ground and provides forage during the winter (Thompson, 1965). A reduction in the number of possible plant food species could account for the vole population removing a large portion of brome grass which forms the major proportion of the litter mat. In the following spring very little litter would be present to retard plant growth.

A greater standing crop of brome grass was noted in the six-year exclosure plots. Whether this is a measure of the decrease of grazing pressure or a response to the absence of other plant species cannot be definitely determined. If the former is true, however, it would imply that brome grass is preventing the other plant species from growing. The grazing by the Microtus population on the brome grass is giving other species the opportunity to occupy the area from which the grass was removed. With the information accumulated by others about the effects of excess litter along with the absence of a significant Bromus weight difference from the first-year exclosure and control, it would be more probable that the increase in the brome grass weight is a response to the absence of other competing plant species. A similar increase in the density of brome grass in the exclosure is probably explained in the same manner. As plants which are not able to adapt to the new set of conditions begin to disappear, brome grass, which is adapted to these conditions, grows in the newly vacated areas.

The difference in the maximum height between the six-year exclosure and control plots is also probably due to a difference in microenvironment, as well as to a response to the absence of competing plant species. Acting as an insulation for both temperature and moisture (Weaver and Rowland, 1952), Bromus is presented with more favorable conditions in the exclosure plots than in the control plots.

Low population densities of Microtus made it difficult to determine the quantities, as well as the particular plant species that this vole population consumed during the year. Data from the first-year exclosure would indicate that the animals seemed to be consuming bluegrass, Poa spp. According to Thompson (1965), this is one of the preferred food species of Microtus. More preferred species listed by Thompson were not, with one exception, present. Taraxcum officinale, dandelion, was present only in limited quantities.

Results in the first-year exclosure experiment indicated that few differences occur during the first year of exclosure under these population densities. Under conditions of peak population densities, the results would undoubtedly be different. The six-year plots represent a longer period of time during which many possible conditions of population densities could act. It, therefore, represents the accumulation of events that have taken place under long-term exclosure.

All the results seen in the six-year exclosure may not be directly attributable to the activities of Microtus. A compound effect is more likely to be present. As conditions slowly change following the initial removal of all Microtus, other animals, which at first found conditions suitable, may, after a period of time, move to the more preferable, unaltered conditions of the control plots. As more animals leave, other changes occur, with the result that the whole community changes more rapidly than before. It would be likely, therefore, that changes occur in both the plant and animal portions of the community (Batzli and Pitelka, 1970). Changes that originally occurred slowly would begin to compound, causing a greater and faster rate of change in the community.

It is doubtful that an equilibrium will be established in the community with brome grass as the only plant species present. As time proceeds, other species able to adapt to the new set of conditions will begin to invade. It is probable that with the invasion of new plant and animal species, a new equilibrium will be established for the community. Whether a new grassland community or the next seral stage will arise cannot be determined in this study. Hope-Simpson (1940) found that woody invaders would come in quickly upon the removal of rabbits from an English grassland community. A longer study would be needed in order to determine the end result of the removal of Microtus.

It was shown in this study that even the removal of a small member of the community, such as the vole, Microtus pennsylvanicus, can cause significant changes throughout the entire community. Microtus, which shows a strong preference for the type of community studied in this experiment (Hodgson, 1970), helps to create its preferred community.

# SUMMARY


1) A decrease in the number of plant species was observed in an area devoid of *Microtus pennsylvanicus* for six years.

2) Along with a decrease in the total number of species was an increase in the degree of dominance of smooth brome grass, *Bromus inermis*.

3) *Microtus* is able to exert its influence through a reduction in the amount of dead plant material that has accumulated from the previous growing season.

4) Studies by other investigators indicate that excessive accumulations of litter cause a lowering of the soil temperature, which retards plant growth by about three weeks.

5) The height of the litter mat excludes any species not able to grow through the mat.

6) Low population densities of *Microtus* made it impossible to determine the amount of the standing crop removed by the grazing of the vole population.

7) Indications were that the vole population was consuming species of bluegrass, genus *Poa*.

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